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MYB transcription factors, active players in abiotic stress signaling

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ABSTRACT

The MYB family of proteins is a group of large, functionally diverse transcription factors, and widely present in all eukaryotes. The MYB family of proteins in plants is characterized by the presence of a conserved MYB DNA-binding domain that typically contains one to four imperfect repeats. In the past decades, extensive information has been accumulated on the roles of these proteins in regulating important processes in plants, including development, metabolism, and responses to environmental stresses. In this review, we summarize the MYB proteins that play crucial roles in plant responses to diverse abiotic stresses, and highlight the possible mechanisms underlying how MYB proteins are regulated at the transcriptional, posttranscriptional and protein levels, and how they regulate downstream target gene networks in association with abiotic stresses.

1. Introduction

The MYB family of transcription factors (TFs) is named by its conserved MYB domain and is present in all eukaryotes. The first identified MYB gene is the *v-Myb* oncogene of an avian myeloblastosis virus (AMV) (Klempnauer et al., 1982). Thereafter, many MYB genes were recognized in animals, plants, fungi and slime molds. The structures and functions of MYB transcription factors in plants are conserved compared with those in animals and yeasts.

The MYB family is one of the largest TF families in plants, representing about 9% of the total TFs in *Arabidopsis* (Riechmann et al., 2000). In *Arabidopsis*, more than 1600 TFs have been identified, accounting for about 6% of the whole genome (Riechmann et al., 2000; Chen et al., 2006). The MYB TFs in plants are characterized by the presence of a highly conserved MYB DNA-binding domain that typically contains one to four imperfect repeats. According to the structure of the DNA-binding domain, they are grouped into four different subfamilies. The first identified gene encoding a MYB domain protein in plants is *COLORED1* (*C1*), which is involved in anthocyanin synthesis in the aleurone layer of maize (*Zea mays*) kernels (Paz-Ares et al., 1987). The presence of numerous MYB proteins in plants implicates that they may individually play unique roles, which have been demonstrated by a large number of studies. It is now clear that MYB proteins function in diverse biological processes including regulation of primary and secondary metabolism, seed and floral development, cell fate and identity, defense and stress responses in plants (Dubos et al., 2010). Here, we review the structures and functions, and emphasize on the possible mechanisms underlying the roles of MYB proteins in responses to abiotic stresses, as well as the possible regulation of MYB gene expression and protein activities in plants.

2. Structure and diversity of the MYB family in plants

The common feature of MYB proteins is the DNA-binding domain (MYB domain), which is generally composed of one to four imperfect repeats (R) in plants (Fig. 1). Each repeat, with about 52 amino acid residues, forms a helix–turn–helix structure with three regularly spaced tryptophan residues in the hydrophobic core that extend into the DNA major groove and mediate recognition of specific DNA sequences (Ogata et al., 1996; Jia et al., 2004). The MYB family is classified into four subfamilies based on the number and position of repeats, namely 4R-MYB, R1R2R3-MYB, R2R3-MYB and 1R-MYB (Dubos et al., 2010).

The 4R-MYB subfamily is the smallest group of the MYB family in plants, each member of which contains four R1/R2 repeats (Fig. 1). Only one 4R-MYB protein was found in several plant species, for example At3g18100 in *Arabidopsis* (Chen et al., 2006). Very little is known about the functions of the members of this subfamily. The R1R2R3-MYB (3R-MYB) subfamily is an evolutionarily conserved group in plants, whose members contain three repeats (Fig. 1), each similar to the vertebrate MYB repeats (Ito, 2005). In contrast to the predominant roles of 3R-MYB group, relatively few 3R-MYB proteins are present amongst plant MYB proteins. For example, there are five genes encoding 3R-MYB

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proteins in *Arabidopsis* and tobacco, and four or five genes in rice (Ito et al., 2001; Stracke, 2001; Dubos et al., 2010; Katiyar et al., 2012).

The R2R3-MYB (2R-MYB) subfamily is the largest group of the plant MYB family, probably evolved from a 3R-MYB ancestor by loss of R1 or from an R1-MYB by duplication (Fig. 1) (Rosinski and Atchley, 1998; Jiang et al., 2004). The 2R-MYB subfamily in plants is classified into three subgroups by phylogenetic analysis, which is consistent with the classification of DNA-binding specificity: subgroup A includes proteins most similar to c-MYB, subgroup B contains proteins encoded by genes with an intron at a conserved position, and subgroup C is the largest group representing genes with an intron at another position (Romero et al., 1998). The structure of 2R-MYB proteins contains two parts: a DNA-binding domain at N terminus and a C-terminal conserved amino acid sequence motif-containing domain. Based on the domains, the 2R-MYB subfamily is categorized into 22 subgroups (Kranz et al., 1998). There are more than 120 members of the 2R-MYB subfamily in *Arabidopsis* and about 90 members in rice (Katiyar et al., 2012). The expansion of 2R-MYB proteins indicates that they may play essential roles in plant-specific processes, which is consistent with studies in the past decade. 2R-MYB proteins have been demonstrated to be involved in the regulation of metabolism, development, cell fate and identity, hormone pathways and responses to stresses in plants. For example, 2R-MYB proteins such as ZmC1, production of anthocyanin pigment 1–4 (PAP1–4) (namely AtMYB75, AtMYB90, AtMYB113, AtMYB114), TT2 (AtMYB123), VvMYBPA2 and VvMYBA2 regulate anthocyanin and proanthocyanidin pathways (Paz-Ares et al., 1987; Borevitz et al., 2000; Nesi et al., 2001; Gonzalez et al., 2008; Heppel et al., 2013); AtMYB7 functions as a repressor of flavonol biosynthesis, which is down-regulated by AtMYB4 (Fornalé et al., 2014).

The 1R-MYB subfamily, also called MYB-related group, is a heterogeneous group, which contains proteins with an intact or partial repeat (Fig. 1). This subfamily is divided into several subgroups including CCA1-like, CPC-like, TRF-like, TBP-like, I-box-binding like and other MYB-related proteins (Chen et al., 2006). It is the second largest group of the MYB family, and is widely distributed in plants. There are 64 members in *Arabidopsis*, 70 members in rice (Dubos et al., 2010). MybSt1 of potato, acting as a transcriptional activator, is the first identified MYB-related protein in plants (Baranowskij et al., 1994). Phylogenetic and expression analyses revealed the conservation and diversity of MYB-related genes, and functional studies demonstrated that they regulate plant development and stress responses (Du et al., 2013).

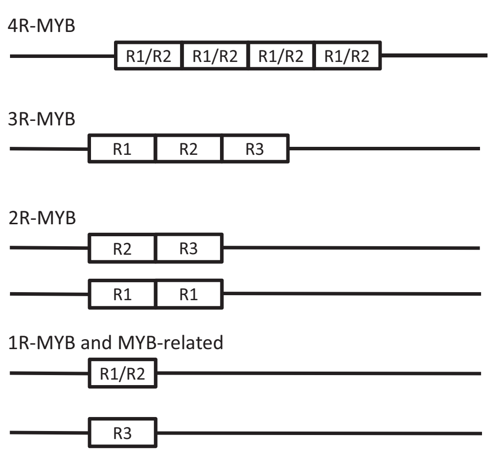

Fig. 1. Illustration of structure and classification of plant MYB transcription factors, showing that their classification depends on the number of adjacent MYB repeats (R).

3. Roles in abiotic stress responses

Plants are challenged by a variety of environmental stresses because they are sessile. Thus, they have evolved numerous strategies to sense and adapt to environmental stresses. Environmental conditions, such as salinity, moisture and temperature, affect plant development, growth and productivity. Therefore, responses and adaptation to abiotic stresses are vital mechanisms for plants to survive. Many genes and proteins are regulated under abiotic stresses, out of which transcription factors are indispensable. As one of the largest TF groups in plants, the MYB family has been shown to be essential for the responses to abiotic stresses (Dubos et al., 2010).

3.1. Drought stress

Drought is a major abiotic stress that negatively affects vegetative and reproductive development of plants, and reduces plant productivity. Expression of many MYB genes has been shown to be responsive to drought stress, and may be involved in drought responses in plants. Genome-wide transcriptomic and microarray analyses have shown that many MYB proteins and MYB-binding element-containing genes are responsive to drought in *Arabidopsis thaliana*, *Zea mays*, *Gossypium herbaceum*, *Macrotyloma uniflorum*, *Malus pumila*, *Populus euphratica*, *Musa* and *Glycine max* (Jia et al., 2006; Davey et al., 2009; Golldack et al., 2011; Pereira et al., 2011; Ranjan et al., 2012; Yan et al., 2012; Bhardwaj et al., 2013; Cao et al., 2013).

In *Arabidopsis*, the stress-induced accumulation of flavonoids was shown to be a positive response to drought stress (Koops et al., 2011). Overexpression of *PAP1* or *MYB12*, two flavonol synthesis regulators, results in less water loss (Nakabayashi et al., 2014). Many R2R3-MYB proteins in *Arabidopsis* have been identified to participate in drought responses. For example, MYB60, a regulator of stomatal movement, is down-regulated by drought stress, and its overexpression results in hypersensitivity to water deficiency (Oh et al., 2011). MYB96, MYB15 and MYB2, induced by drought, act as positive regulators of drought tolerance by activating the transcription of dehydration responsive genes, such as *RD22* (Urao et al., 1996; Abe et al., 2003; Ding et al., 2009; Seo et al., 2009). The biosynthesis of cuticular wax activated by MYB96 is required for the drought tolerance of plants (Seo et al., 2009, 2011). Flu-like protein (FLP) and MYB88, important for normal stomata production, were shown to positively modulate stress responsive genes and drought responses (Xie et al., 2010). AtMYB41 is induced by drought and may function as a transcription factor in modulating cell expansion and cuticle deposition during drought stress (Cominelli et al., 2008b). *MYB44* overexpression confers drought resistance to *Arabidopsis* plants by repressing protein phosphatase 2C (PP2C) genes (Jung et al., 2008). Botrytis susceptible1 (BOS1) and AtMYB102 were also shown to be positive regulators of drought tolerance (Denekamp and Smeekens 2003; Mengiste et al., 2003).

In addition to MYB proteins in *Arabidopsis*, several MYB proteins have also been found to be involved in drought responses in other species. In apple, *MdoMYB121* is induced by drought stress and its overexpression in tomato and apple confers improved tolerance (Cao et al., 2013). *MdSIMYB1*, induced by drought and other abiotic stresses, positively controls the drought resistance by inducing stress and auxin responsive genes (Wang et al., 2014). In rice, *OsMYB4*, *OsMYB3R-2* and *OsMYB2* are induced by drought, and their ectopic expression facilitates drought resistance (Mattana et al., 2005; Dai et al., 2007; Pasquali et al., 2008; Yang et al., 2012a). The *OsMYB59* promoter contains a *DRE cis*-element, and *OsMYB59* is positively regulated by heterogeneous expression of tomato stress-responsive factor1 (*TSRF1*), indicating that *OsMYB59* plays a

positive role in drought tolerance (Quan et al., 2010). In wheat, *TaMYB3R1*, *TaMYB1* and *TaMYBsdu1* are induced by PEG or drought treatment, implicating their roles in drought responses (Lee et al., 2006; Rahaie et al., 2010; Cai et al., 2011). *TaPIMP1* is up-regulated and transgenic tobacco displays enhanced tolerance during drought stress (Liu et al., 2011). Expression of *TaMYB30* and its homologues is induced in response to PEG stress, and over-expression of *TaMYB30-B*, one of three homologues, improves drought tolerance of transgenic *Arabidopsis* (Zhang et al., 2012b). Transgenic *Arabidopsis* plants overexpressing *TaMYB33* and *TaMYB2A* also display drought resistance (Mao et al., 2011; Qin et al., 2012). Suppression of an ARP protein nicotiana benthamiana phantastica (NbPHAN) that belongs to the R2R3-MYB subfamily leads to impaired drought tolerance in *Nicotiana benthamiana* (Huang et al., 2013). *VvMYB60* in grapevine, *StMYB1R-1* in potato and *CmMYB2* in *Chrysanthemum* are up-regulated by drought stress, and their constitutive expression confers drought resistance (Galbiati et al., 2011; Shin et al., 2011; Shan et al., 2012). Soybean *GmMYB177* is induced by drought but not abscisic acid (ABA) treatment, which indicates that *GmMYB177* may play a role in the ABA-independent drought signaling pathway (Liao et al., 2008). Interestingly, a cross-talk exists between drought responses and flower development. MYB genes involved in anther development, including *MYB33, MYB35, MYB65, MYB80, MYB99, MYB110*, are repressed, but *MYB21*, a filament elongation positive regulator, is induced by drought stress. This fact is in agreement with the observation that drought caused retardation of anther development (Wijeratne et al., 2007; Su et al., 2013).

3.2. Salt stress

Excess salt is another major stress which causes ion imbalance and water deficiency. As water deficiency is also induced by drought stress, there are many regulators linking salt and drought stress responses (Golldack et al., 2011). Some MYB proteins have similar effects in drought and salt responses, such as *TaMYB2A, TaMYB3R1, TaMYB33, TaPIMP1, TaMYB1, TaMYBsdu1, GmMYB177, OsMYB3R-2, OsMYB2, MdSIMYB1, MdoMYB121, AtMYB44, AtMYB2, AtFLP, AtMYB88, AtMYB41* and *CmMYB2* (Yoo et al., 2005; Lee et al., 2006; Dai et al., 2007; Cominelli et al., 2008b; Liao et al., 2008; Jung et al., 2008; Rahaie et al., 2010; Xie et al., 2010; Cai et al., 2011; Liu et al., 2011; Mao et al., 2011; Qin et al., 2012; Shan et al., 2012; Yang et al., 2012a; Cao et al., 2013; Wang et al., 2014). AtMYB20 enhances salt resistance by repression of PP2Cs expression (Cui et al., 2013). AmMYB1 from the salt-tolerant *Avicennia marina* binds and transactivates *AtRD22* in yeast cells and improves the salt tolerance of transgenic tobacco (Ganesan et al., 2012). TaMYB73 confers enhanced ionic resistance-based salt tolerance by regulating the expression of stress related genes (He et al., 2012). Microarray assays in *Medicago truncatula* showed that *MYB119*, *MYB634* and *MYB636* are induced in the root apex but *MYB1070* is induced in whole roots, under salt stress (Gruber et al., 2009), suggesting possible tissue or organ-specificity of different MYB proteins under salt stress. AtMYB73 acts as a negative regulator of salt responses by suppression of salt overly sensitive (*SOS*) genes (Kim et al., 2013). TaMYB56-B and LcMYB1 were shown to positively modulate stress responsive genes and salt responses in transgenic *Arabidopsis* (Zhang et al., 2012a; Cheng et al., 2013). A 1R-MYB protein AtHPPBF-1 physically interacts with STO that regulates internal Na^+/K^+ ratio to control salt responses (Nagaoka and Takano 2003). Microarray analysis revealed that four MYB proteins in soybean are induced during salt stress, and epigenetic modification assays showed that salt stress regulates *Glyma11g02400* by transcriptional activation and methylation reduction (Song et al., 2012). *GmMYB76* and *GmMYB92* are induced by salt treatment in an ABA independent pathway (Liao et al., 2008). *Arabidopsis bos1* mutant is hypersensitive to drought, salt and oxidative stress, suggesting that BOS1 is a positive regulator of the abiotic stress responses (Mengiste et al., 2003).

3.3. Temperature stress

Temperature is an important environmental factor that affects plant growth and development. Temperature stresses include cold, freezing and heat. Expression data from different plants species have indicated that the members of the MYB family participate in plant responses to temperature stresses (Rensink et al., 2005; Lim et al., 2006; Bedon et al., 2010; Yun et al., 2010; Jiang et al., 2013; Tian et al., 2013). *OsMYB4* is induced by cold stress, and *OsMYB4* overexpressing lines of *Arabidopsis* are tolerant to cold and freezing stresses (Pasquali et al., 2008). AtMYB15 acts as a negative regulator of freezing tolerance by suppressing the expression of *CBF1/DREB1* (Agarwal et al., 2006). An *Arabidopsis* MYB gene *arabidopsis reveille1* (*AtRVE1*) that was QTL mapped and cloned, negatively modulates freezing tolerance (Meissner et al., 2013). AtMYBC1, a 1R-MYB protein, is a repressor of freezing tolerance in a CBF independent pathway (Zhai et al., 2010). OsMYBS3 was identified as a positive regulator of cold tolerance, but represses the DREB1/CBF-dependent cold signaling pathway in rice, indicating that distinct pathways act sequentially and complementarily for adapting short- and long-term cold stress (Su et al., 2010). Transgenic plants that overexpress *MYB family transcription factorcircadian1* (*AtCIR1*) display increased expression of *CBF* genes and increased tolerance to freezing stress before and after cold acclimation, indicating that AtCIR1 positively regulates cold responsive genes and cold tolerance (Guan et al., 2013). Anthocyanin synthesis is influenced by temperature stresses in plants. For example, low temperatures induce and high temperatures suppress anthocyanin biosynthesis in *Arabidopsis*, which involves the altered regulation of *AtMYB3*, *AtMYB6* and *AtMYBL2* (Leyva et al., 1995; Rowan et al., 2009). Apple MYB10 is responsible for the temperature affected anthocyanin accumulation (Lin-Wang et al., 2011). PcMYB10 in pears positively controls low temperature-induced anthocyanin synthesis (Li et al., 2012). Based on these data, it is pertinent to propose that MYB proteins may be involved in the correlation between anthocyanin accumulation and cold tolerance. However, whether anthocyanin accumulation leads to increased cold tolerance remains to be conclusively determined.

In addition to the information regarding MYB proteins in temperature responses, there are also some data showing that MYB proteins are involved in the cross-talk between cold, salt and drought stress responses. For example, MYB proteins in different species such as MdoMYB121, MdSIMYB1, TaMYB3R1, OsMYB3R-2, OsMYB2, AtMYB44, TaMYB2A, LcMYB1 regulate cold, salt and drought stress responses (Dai et al., 2007; Jung et al., 2008; Mao et al., 2011; Cai et al., 2011; Yang et al., 2012a; Cao et al., 2013; Cheng et al., 2013; Wang et al., 2014), GmMYB92 and TaMYB56-B control salt and cold responses (Liao et al., 2008; Zhang et al., 2012a), while OsMYB4 modulates drought and cold responses (Pasquali et al., 2008). It is thus plausible that MYB proteins may be a key regulatory node of plant responses to multiple abiotic stresses.

3.4. Pi starvation

Phosphorus (Pi) is one of the major elements of plants, and is absorbed from soil by roots. Pi limitations result in the retardation of plant growth, development and productivity (Nilsson et al., 2010). In turn, plants have evolved adaptive strategies to respond to limited Pi supply from soil. MYB proteins have been shown to be part of the mechanisms underlying plant responses to Pi starvation. The first MYB protein found to be involved in the Pi starvation pathway is

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chlamydomonas phosphorous starvation resistant1 (*CrPSR1*). Transcriptome studies revealed that *CrPSR1*, induced in response to Pi starvation, regulates many Pi-transport and acquisition genes (Wykoff et al., 1999). Homologues of CrPSR1 in *Arabidopsis*, rice and *Brassica napus* were also shown to be involved in the Pi starvation signaling. Genome-wide analyses have also been performed in other plant species such as *Arabidopsis*, tomato, rice, wild mustard and bean, and showed that several MYB protein genes are induced or repressed by Pi starvation (Wang et al., 2002; Wasaki et al., 2006; Hernandez et al., 2007; Nilsson et al., 2010). The expression of *Arabidopsis* MYB family proteins, *PAP1, PAP2, MYB108, At1g13300, At1g68670* and *At3g25790* were shown to be induced, but MYB111 was repressed in response to Pi starvation (Nilsson et al., 2010). arabidopsis phosphate starvation response 1 (AtPHR1) is a positive regulator of Pi-acquisition and Pi starvation-induced genes (Nilsson et al., 2007), and its transcription does not change apparently but undergoes post-transcriptional modification in response to Pi starvation (Rubio et al., 2001). AtPHR2, a homologue of AtPHR1, is induced in response to Pi deprivation (Todd et al., 2004). AtPHL1, a phylogenetic relative of AtPHR1, is partially functionally redundant to AtPHR1 in Pi starvation responses (Bustos et al., 2010). Overexpression of *OsPHR2* leads to greater accumulation of phosphate as does that of AtPHR1, thereby implicating the involvement of *OsPHR2* in regulating Pi deficiency pathway in rice (Zhou et al., 2008). *BnPHR1* is induced by Pi starvation and activates some PSI genes by binding to their promoter (Ren et al., 2012). R2R3-type MYB TF *AtMYB62* is induced by Pi deficiency, but overexpression of *MYB62* results in the suppression of Pi starvation responses and a gibberellic acid (GA) deficient phenotype, suggesting that MYB62 plays roles in the Pi starvation feedback pathway and in the cross-talk between Pi supply and GA metabolism (Misson et al., 2005; Devaiah et al., 2009). AtMYB2 was recently demonstrated to modulate Pi starvation responses by activating expression of *microRNA399*, an essential regulator in Pi starvation signaling (Baek et al., 2013). OsMYB2P-1, a 2R-type MYB protein in rice, positively regulates the Pi starvation signaling by controlling the uptake and translocation of Pi (Dai et al., 2012).

3.5. Metal stress

Very few studies have been carried out to investigate the involvement of the MYB family in metal stress responses in plants, which mainly focus on iron and aluminum stresses. Iron is an essential element for plant photosynthesis and respiration. Genome-wide transcripts analyses revealed that two MYB proteins in rice and two in *Arabidopsis* are induced under iron deficiency (Colangelo and Guerinot 2004; Sperotto et al., 2008; Palmer et al., 2013). In *Malus xiaojinensis*, an apple species tolerant to low iron condition, *MxMYB1* is induced and acts as a negative regulator of iron transport and storage under Fe deficiency (Shen et al., 2008). Overexpression of the orchid 2R-MYB gene *DwMYB2* makes *Arabidopsis* hypersensitive to iron deficiency by regulating many iron transport genes (Chen et al., 2006). Aluminum toxicity is a major soil constraint for plant growth and development in acid soils (Horst et al., 2010). Many MYB proteins involved in ABA signaling and drought responses have been found to be regulated by aluminum stress in common bean (*Phaseolus vulgaris*) (Yang et al., 2012b). MicroRNAs were demonstrated to be essential for response to aluminum stress by mediating the cleavage of many mRNA targets encoded by MYB transcription factor genes in wild soybean (Zeng et al., 2012).

3.6. Sugar stress

Sugars, such as maltose, sucrose, fructose and glucose, function as signaling molecules for plant growth and development, in addition to their important roles in plant metabolism and energy homeostasis. Inappropriate concentration of sugar may cause stress to plants, which affects the development of plants (Ohto et al., 2001). Sugars were shown to induce anthocyanin biosynthetic genes and the accumulation of anthocyanin, which is mediated by the MYB-BHLH-WD40 complex (Mita et al., 1997; Baier et al., 2004; Solfanelli et al., 2006). The study of *Arabidopsis pho3* mutant revealed that sugars trigger the expression of two MYB genes *PAP1* and *PAP2* (Lloyd and Zakhleniuk 2004), and another research suggested that the sugar signaling pathway up-regulating *PAP1* is sucrose specific in *Arabidopsis* (Solfanelli et al., 2006). The transcriptional level and mRNA stability of α-amylase genes in cereals are also regulated by sugars. Sugar starvation activates but sugar provision represses the expression of α-amylase genes in rice suspension cells, germinating rice embryos and barley seeds (Su-May et al., 1992; Yu et al., 1996; Perata et al., 1997; Yu 1999). It has been shown that three 1R-MYB proteins in rice, OsMYBS1, OsMYBS2 and OsMYBS3, play essential roles in the sugar regulation of α-amylase. *OsMYBS1* and *OsMYB3* are repressed, but *OsMYBS2* is induced by sugar (Lu et al., 2002). They may form a complex to respond to sugar stress (Lu et al., 2002). Another study showed that transgenic *Arabidopsis* overexpressing *CpMYB10* is tolerant to high sorbitol stress and insensitive to glucose (Villalobos et al., 2004). The above data together support the notion that MYB proteins play roles in sugar responses.

3.7. Light stress

Light is one of the most vital environmental elements controlling plant growth and development. Light stresses, such as damaging ultraviolet and differential light qualities irradiation, affect the synthesis of sunscreen flavonols in plants. Many R2R3-MYB proteins in *Arabidopsis* are regulated in response to differential light qualities (Cominelli et al., 2008a). DcMYB1 is required for UV-B irradiation-induced *DcPAL1* by binding to the promoter of *DcPAL1* in carrot (Maeda et al., 2005). *Production of flavonol glycosides 1* (*PFG1*)/*AtMYB12* and *PFG3/AtMYB111* genes are activated under UV-B, and overexpression of *PFG1* confers an increased UV-B tolerance in *Arabidopsis* (Stracke et al., 2010). AtMYB4 acts as a negative regulator of UV-B tolerance, whose expression is repressed by UV-B but induced by UV-A irradiation, and AtMYB7 expression is repressed by AtMYB4, which contributes to the UV sunscreen regulation (Jin et al., 2000; Fornalé et al., 2013). Expression of *PAP1, MYB4, MYB12* and *MYB111* in the turnip *Brassica rapa* is regulated by different light spectra, suggesting their roles in response to light stress (Wang et al., 2012). As a *CHS* promoter binding protein, the R2R3-type MYB gene *pericarp color1* (*P1*), expressed in leaves, positively controls UV-B tolerance in high-altitude maize (Rius et al., 2012). *AtPAP1* and *AtPAP2*, two major MYB transcription factors in anthocyanin biosynthesis, are induced by high light stress and play important roles in the regulation of high light driven anthocyanin synthesis (Vanderauwera et al., 2005). *HbMYB1* is also involved in UV-B stress, evidenced by the fact that *HbMYB1* overexpression in tobacco leads to enhanced resistance to UV-B stress (Peng et al., 2011).

3.8. Wounding stress

As sessile organisms, plants have to protect themselves from wounding stress by regulating defense systems-related genes. Several regulatory pathways that are involved in the wounding responses involve calcium ions, ABA, jasmonic acid (JA), ethylene, fatty acids, hydrogen peroxide and systemin (Knight et al., 1993; Ryu and Wang 1998; Rojo et al., 1999; Orozco-Cardenas and Ryan 1999; Ryan 2000). Many MYB proteins involved in

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Table 1
MYB proteins involved in abiotic stress in plants.

Plant species	Name	Accession number	Subfamily	Abiotic stress	Reference
Arabidopsis thaliana	MYB2	AT2G47190	R2R3-MYB	Drought, salt, Pi starvation, anoxia	Abe et al., 2003; Baek et al., 2013; Hoeren et al., 1998; Urao et al., 1996
	MYB3	AT1G22640	R2R3-MYB	High temperature	Rowan et al., 2009
	MYB4	AT4G38620	R2R3-MYB	UV	Jin et al., 2000
	MYB6	AT4G09460	R2R3-MYB	High temperature	Rowan et al., 2009
	MYB7	AT2G16720	R2R3-MYB	UV-B	Fornalé et al., 2014
	MYB12	AT2G47460	R2R3-MYB	Drought, UV-B	Nakabayashi et al., 2013; Stracke et al., 2010
	MYB13	AT1G06180	R2R3-MYB	Boric acid	Nozawa et al., 2006
	MYB15	AT3G23250	R2R3-MYB	Drought, freezing stress	Agarwal et al., 2006; Ding et al., 2009
	MYB20	AT1G66230	R2R3-MYB	Salt	Cui et al., 2013
	MYB21	AT3G27810	R2R3-MYB	Drought	Su et al., 2013
	MYB33	AT5G06100	R2R3-MYB	Drought	Su et al., 2013
	MYB35	AT3G28470	R2R3-MYB	Drought	Su et al., 2013
	MYB41	AT4G28110	R2R3-MYB	Drought, salt	Cominelli et al., 2008b
	MYB44	AT5G67300	R2R3-MYB	Drought, salt, cold	Jung et al., 2008
	MYB60	AT1G08810	R2R3-MYB	Drought	Oh et al., 2011
	MYB62	AT1G68320	R2R3-MYB	Pi starvation	Devaiah et al., 2009
	MYB65	AT3G11440	R2R3-MYB	Drought	Su et al., 2013
	MYB68	AT5G65790	R2R3-MYB	Boric acid	Nozawa et al., 2006
	MYB73	AT4G37260	R2R3-MYB	Salt	Kim et al., 2013
	PAP1/MYB75	AT1G56650	R2R3-MYB	Drought, sugar, Pi starvation, UV-A, high light, nitrogen deficiency	Feyissa et al., 2009; Nakabayashi et al., 2013; Nilsson et al., 2010; Solfanelli et al., 2006; Vanderauwera et al., 2005; Wang et al., 2012
	MYB80	AT5G56110	R2R3-MYB	Drought	Su et al., 2013
	MYB88	AT2G02820	R2R3-MYB	Drought, salt	Xie et al., 2010
	PAP2/MYB90	AT1G66390	R2R3-MYB	Sugar, Pi starvation, high light, nitrogen deficiency	Feyissa et al., 2009; Lloyd and Zakhleniuk, 2004; Nilsson et al., 2010; Vanderauwera et al., 2005
	MYB96	AT5G62470	R2R3-MYB	Drought	Seo et al., 2009 2011
	MYB99	AT5G62320	R2R3-MYB	Drought	Su et al., 2013
	MYB102	AT4G21440	R2R3-MYB	Drought, wound	Denekamp and Smeekens, 2003
	BOS1/MYB108	AT3G06490	R2R3-MYB	Drought, salt, Pi starvation, oxidative stress	Mengiste et al., 2003; Nilsson et al., 2010;
	MYB110	AT3G29020	R2R3-MYB	Drought	Su et al., 2013
	MYB111	AT5G49330	R2R3-MYB	Pi starvation, UV-B	Nilsson et al., 2010; Wang et al., 2012
	FLP/MYB124	AT1G14350	R2R3-MYB	Drought, salt	Xie et al., 2010
	HPPBF-1	AT5G13820	MYB related protein	Salt	Nagaoka and Takano, 2003
	RVE1	AT5G17300	MYB related protein	Freezing stress	Meissner et al., 2013
	MYBC1	AT2G40970	MYB related protein	Freezing stress	Zhai et al., 2010
	CIR1	AT5G37260	MYB related protein	Cold	Guan et al., 2013
	MYBL2	AT1G71030	MYB related protein	High temperature	Rowan et al., 2009
	At1g13300		MYB related protein	Pi starvation	Nilsson et al., 2010
	At1g68670		MYB related protein	Pi starvation	Nilsson et al., 2010
	At3g25790		MYB related protein	Pi starvation	Nilsson et al., 2010
	PHR1	AT1G12370	MYB related protein	Pi starvation	Rubio et al., 2001
	PHR2	At1g79430	MYB related protein	Pi starvation	Todd et al., 2004
	PHL1	AT5G29000	MYB related protein	Pi starvation	Bustos et al., 2010
	CCA1	AT2G46830	MYB related protein	Pi starvation	Daniel et al., 2004; Lin et al., 2013a
	NSR1	At3g04030	MYB related protein	Nitrogen deficiency	Todd et al., 2004
Apple	MdoMYB121 (*Malus* × *domestica*)	KC834015	R2R3-MYB	Drought, salt, cold	Cao et al., 2013
	MdSIMYB1 (*Malus* × *domestica*)	KC691248	R2R3-MYB	Drought, salt, cold	Wang et al., 2014
	MYB10 (*Malus* × *domestica* Borkh.)	EU518249	R2R3-MYB	Temperature stress	Lin-Wang et al., 2011
	MxMYB1 (*Malus xiaojinensis*)	AAO45179	MYB related protein	Fe deficiency	Shen et al., 2008
Rice (*Oryza sativa*)	MYB2	AK120551	R2R3-MYB	Drought, salt, cold	Yang et al., 2012a
	MYB4	Y11414	MYB related protein	Drought, freezing stress	Pasquali et al., 2008
	MYB3R-2	BAD81765	R1R2R3-MYB	Drought, salt, cold	Dai et al., 2007
	MYB59	AY569615	R2R3-MYB	Drought	Quan et al., 2010

Table 1 (*Continued*)

Plant species	Name	Accession number	Subfamily	Abiotic stress	Reference
	MYBS1	AY151042	MYB related protein	Sugar	Lu et al., 2002
	MYBS2	AY151043	MYB related protein	Sugar	Lu et al., 2002
	MYBS3	AY151044	MYB related protein	Cold, sugar	Lu et al., 2002; Su et al., 2010
	PHR2	AK100065	MYB related protein	Pi starvation	Zhou et al., 2008
	MYB2P-1	Os.9514.1. S1_at	R2R3-MYB	Pi starvation	Dai et al., 2012
	Mybleu	X89605	MYB related protein	oxygen deficiency	Mattana et al., 2007
	MPS	Os02g40530	R2R3-MYB	Salt	Schmidt et al., 2013
Wheat (*Triticum aestivum*)	MYB1	DN828996	R2R3-MYB	Drought, salt	Lee et al., 2006
	MYB2A	AY615199	R2R3-MYB	Drought, salt, cold	Mao et al., 2011
	MYB3R1	HQ236494	R1R2R3-MYB	Drought, salt, cold	Cai et al., 2011
	MYBsdu1	BT008981	R2R3-MYB	Drought, salt	Rahaie et al., 2010
	PIMP1	CN011324	R2R3-MYB	drought, salt	Liu et al., 2011
	MYB30	JF951913	R2R3-MYB	Drought	Zhang et al. 2012b
	MYB33	JN584645	R2R3-MYB	Drought, salt	Qin et al., 2012
	MYB56-B	JX183617	MYB related protein	Salt, cold	Zhang et al., 2012a
	MYB73	JN969051	R2R3-MYB	Salt	He et al., 2012
Nicotiana benthamiana	NbPHAN	FR878011	R2R3-MYB	Drought	Huang et al., 2013
Grapevine (*Vitis vinifera*)	VvMYB60	ACF21938	R2R3-MYB	Drought	Galbiati et al., 2011
Potato (*Solanum tuberosum*)	StMYB1R-1	AU279205	MYB related protein	Drought	Shin et al., 2011
Chrysanthemum	CmMYB1	JF795917	R2R3-MYB	Nitrogen deficiency	Imamura et al., 2009
	CmMYB2	JF795918	R2R3-MYB	Drought, salt	Shan et al., 2012
Soybean (*Glycine max*)	GmMYB177	DQ822925	MYB related protein	Drought, salt	Liao et al., 2008
	Glyma11g02400			Salt	Song et al., 2012
	GmMYB76	DQ822895	R2R3-MYB	Salt	Liao et al., 2008
	GmMYB92	DQ822903	R2R3-MYB	Salt, cold	Liao et al., 2008
Avicennia marina	AmMYB1	EU091320	MYB related protein	Salt	Ganesan et al., 2012
Medicago truncatula	MYB119			Salt	Gruber et al., 2009
	MYB634			Salt	Gruber et al., 2009
	MYB636			Salt	Gruber et al., 2009
	MYB1070			Salt	Gruber et al., 2009
Sheepgrass (*Leymus chinensis*)	LcMYB1	KC154048	MYB related protein	Salt, cold	Cheng et al., 2013
Pear (*Pyrus communis*)	PcMYB10	EU153575	R2R3-MYB	Low temperature	Li et al., 2012
Craterostigma plantagineum	CpMYB10	AF510112		Sugar,salt,drought	Villalobos et al., 2004
Chlamydomonas	CrPSR1	AF174532	MYB related protein	Pi starvation	Wykoff et al., 1999
Brassica napus	BnPHR1	JN806156	MYB related protein	Pi starvation	Ren et al., 2012
Orchid (*Dendrobium hybrid*)	DwMYB2	AF485893	R2R3-MYB	Iron deficiency	Chen et al., 2006a
Poplar (*Populus*)	MYB134	FJ573151	R2R3-MYB	Wound	Mellway et al., 2009
Persimmon (*Diospyros kaki*)	DkMYB2	AB503699	R2R3-MYB	Wound	Akagi et al., 2010
	DkMYB4	AB503701	R2R3-MYB	Wound	Akagi et al., 2010
Sweet potato (*Ipomoea batatas*)	IbMYB1	KC166234	R2R3-MYB	Wound	Lin et al., 2013b
	IbMYB2	HF937132	R2R3-MYB	Wound	Lin et al., 2013b
Tobacco (*Nicotiana tabacum*)	NtMYB2	AB028649	R2R3-MYB	Wound	Sugimoto et al., 2000
Saccharum officinarum	ScMYBAS1	EU670236		Wound, salt, drought	Prabu and Prasad, 2012
Carrot (*Daucus carota*)	DcMYB1	AB218778	R2R3-MYB	UV-B	Maeda et al., 2005
Turnip (*Brassica rapa*)	BrMYB12	HQ317142	R2R3-MYB	UV-A	Wang et al., 2012
	BrMYB111	HQ317140	R2R3-MYB	UV-A	Wang et al., 2012
Maize (*Zea mays*)	P1	AY702552	R2R3-MYB	UV-B	Rius et al., 2012
Hevea brasiliensis	HbMYB1		MYB related protein	UV-B, paraquat	Peng et al., 2011

proanthocyanidin biosynthesis are induced by wound stress, such as TT2-like *MYB134* in poplar, *DkMYB2* and *DkMYB4* in persimmon (Mellway et al., 2009; Akagi et al., 2010). The expression of AtMYB102, an *Arabidopsis* MYB protein, is activated under wounding and osmotic stresses, and may act as an integrator of wounding and osmotic stresses (Denekamp and Smeekens 2003). Wounding causes the sRNA8105-mediated suppression of *lbMYB1* gene family members that are regulators of phenylpropanoid pathway (Lin et al., 2013b). Another experiment further showed that *lbMYB* may be microRNA828 targets in wounding responses in sweet potato (Lin et al., 2012; Lin et al., 2013b). *NtMYB2* is induced by wounding and regulates defense-related genes and retrotransposons in tobacco (Sugimoto et al., 2000). Transcription of *ScMYBAS1* is induced in response to wound stress, which is revealed by the characterization of its promoter in tobacco (Prabu and Prasad 2012).

3.9. Other abiotic stresses including anoxia, nitrogen deficiency and boron stress

In addition to playing roles in the responses of stresses discussed above, some lines of fragmental evidence indicate that MYB proteins are also involved in other stress responses.

AtMYB2 binds to a *Myb*-box motif of anaerobically induced genes to regulate the anoxia response in *Arabidopsis* (Dolferus et al., 2003). Rice *Mybleu* is expressed under aerobic conditions, and its constitutive expression enhances tolerance to oxygen deficiency (Mattana et al., 2007). Expression of several other rice MYB genes including *Os02g0706400, Os06g0728700, Os08g0151000, Os01g0524500, Os01g0863300, Os08g0549000, Os05g0459000* and *Os04g0480300* is enhanced during rice anoxic germination (Mohanty et al., 2012).

AtNSR1 is up-regulated under nitrogen deficiency, and regulates expression of nitrate responsive genes (Todd et al., 2004). Nitrogen depletion-induced anthocyanin biosynthesis involves many major regulators of anthocyanin pathway including MYB proteins PAP1 and PAP2 (Feyissa et al., 2009). Phenotypic analysis of *CmMYB1* null mutant suggests that CmMYB1 is a central positive regulator of nitrogen depletion response in *Cyanidioschyzon merolae* (Imamura et al., 2009).

Overexpression of two MYB transcription factors *AtMYB13* and *AtMYB68* in *Saccharomyces cerevisiae* confers high tolerance to boric acid (Nozawa et al., 2006). Interestingly, 49% of barley MYB TFs are down-regulated and 33% are up-regulated in boron-induced roots, and 37% induced and 25% repressed in leaves (Tombuloglu et al., 2013). These observations suggest that MYB proteins may also play roles in boron responses.

4. MYB-regulated gene networks in abiotic stress responses

MYB proteins are shown to be involved in the regulation of numerous stress-related genes directly or indirectly in response to abiotic stresses. Many factors have been found to be regulated by and act downstream of MYB proteins. These findings have contributed to our understanding of the mechanisms underlying the functioning of MYB proteins in abiotic stresses. These downstream factors involve RD22, SOSs, PP2Cs, Pi transporters, ROS scavenging proteins, ABA synthesis proteins, cell expansion and cuticle metabolism proteins and other stress-induced proteins (Cominelli et al., 2008b; Jung et al., 2008; Seo et al., 2009; Dai et al., 2012; Qin et al., 2012; Kim et al., 2013). Some information regarding direct target genes for several MYB proteins has been provided in the platform AtRegNet (Palaniswamy et al., 2006).

Anthocyanins are flavonoid pigments in plants and protect plants from abiotic stresses. Diverse abiotic stresses cross-talk with one another in the regulation of anthocyanin biosynthesis, in which MYB proteins play essential roles by regulating the expression of a large number of anthocyanin biosynthetic genes. For example, the expression of early anthocyanin biosynthetic genes is modulated by MYB12/PFG1, MYB11/PFG2 and MYB111/PFG3, while some late anthocyanin biosynthetic genes are regulated by MYB75/PAP1, MYB90/PAP2, MYB113 and MYB114 (Hichri et al., 2011). Some anthocyanin biosynthetic genes are even the direct targets of MYB proteins in response to abiotic stresses. DcMYB1 binds to the box-L-like sequences of *DcPAL1* promoter specifically and activates *DcPAL1* under UV-B irradiation (Maeda et al., 2005). Overexpression of *OsMYB4* in transgenic *Arabidopsis* increases freezing tolerance by transactivating *PAL2* and other cold inducible genes (Vannini et al., 2004). MYB134 in poplar, which is essential for wound and UV-B tolerance, regulates stress-responsive proanthocyanidin biosynthesis by binding to the promoter of proanthocyanidin biosynthetic genes, such as *peroxisomal abc transporter-like protein1* (*PAL1*) and *anthocyanidin reductase2* (*ANR2*) (Mellway et al., 2009). NtMYB2 activates phenylpropanoid biosynthesis by binding to the *PAL* gene promoter in response to wounding stress (Sugimoto et al., 2000). DkMyb2 is a wound-induced transcription factor regulating proanthocyanidin synthesis by direct transcriptional activation of *DkANR* and *DkLAR* (Akagi et al., 2010).

In addition to the anthocyanin biosynthetic genes, many stress related genes were also shown to be the targets of MYB proteins in response to abiotic stresses. For example, AtMYB2 acts as a transcriptional activator that binds to the promoter of *AtRD22* under drought stress, binds to GT-motif of *alcohol dehydrogenase 1* (*ADH1*) promoter in response to low oxygen and activates miR399 mediating the degradation of *phosphate overaccumulator* (*PHO2*) mRNA to induce the expression of Pi starvation induced genes under Pi deficiency stress (Abe et al., 2003; Baek et al., 2013; Hoeren et al., 1998). AtMYB96 regulates cuticular wax biosynthesis to enhance drought tolerance by binding to the promoters of wax biosynthetic genes*3-ketoacyl-CoA synthase* (*KCS*) *1, 2* and *6, KCR1, eceriferum1cer3,* and *beta-ketoacyl reductase1* (*WSD1*) (Seo et al., 2011). AtMYB15 is a negative regulator of cold tolerance which binds to the promoters of *CBF* genes (Agarwal et al., 2006). AtMYB20 represses the expression of PP2Cs and enhances salt tolerance by binding to the promoter of *ABA insensitive1* (*ABI1*) and *PP2CA*, which are negative regulators of ABA signaling (Cui et al., 2013). The regulation of cell cycle mediated cold tolerance in rice involves OsMYB3R-2 targeting cyclin genes such as *OsCycB1;1*, which has two mitosis-specific activator cis-elements in its promoter (Ma et al., 2009). RICE MULTIPASS (OsMPS) plays important roles in the response to abiotic stresses in rice by directly modulating the expansin and endoglucanase genes (Schmidt et al., 2013). Transient expression assays showed that OsMYBS proteins regulate α-amylase genes by binding to their TATCCA element to respond to sugar stress (Lu et al., 2002). CmMYB1 in *Cyanidioschyzon merolae* acts as a positive regulator in response to nitrogen depletion by binding to the promoter of itself and nitrogen assimilation genes, such as *CmNRT*, *CmNIR* and *CmGS* (Imamura et al., 2009). AtPHR1 and AtPHL1 function redundantly to regulate Pi starvation response by binding to the cis-acting P1BS (PHR1-binding sequence) element of Pi starvation-induced genes such as *AtIPS1* (Rubio et al., 2001). BnPHR1 binds to the promoter of *PT2*, which is a high affinity Pi transporter to regulate Pi homeostasis (Ren et al., 2012). *NAC019*, a regulator of abiotic stress, is the direct target downstream of FLP/MYB88 (Xie et al., 2010).

5. Regulation of MYB functions in abiotic stress responses

A large number of MYB protein genes are induced or repressed in response to diverse abiotic stresses. Yet the underlying

Table 2
Targets of MYB proteins involved in response to abiotic stresses.

MYB proteins	Direct targets of MYB proteins	Reference
AtMYB2	*RD22*,*ADH1* and *miR399*	Abe et al., 2003; Baek et al., 2013; Hoeren et al., 1998
AtMYB15	*CBF3*	Agarwal et al., 2006
AtMYB20	*ABI1 and PP2CA*	Cui et al., 2013
AtMYB96	*KCS1, KCS2, KCS6, KCR1, CER3* and *WSD1*	Seo et al., 2011
AtMYBL2	*DFR*	Matsui et al., 2008
AtPHR1 and AtPHL1	*IPS1*	Rubio et al., 2001
MYB134 in poplar	*PAL1* and *ANR2*	Mellway et al., 2009
BnPHR1	*PT2*	Ren et al., 2012
FLP and MYB88	*NAC019*	Xie et al., 2010
AmMYB1	*AtRD22*	Ganesan et al., 2012
OsMYB3R-2	*OsCycB1;1*	Ma et al., 2009
OsMYB4	*PAL2, ScD9 SAD and COR15a*	Vannini et al., 2004
OsMPS	Expansin and endoglucanase genes	Schmidt et al., 2013
OsMYBS1/2/3	*α-amylase gene*	Lu et al., 2002
DcMYB1	*DcPAL1*	Maeda et al., 2005
NtMYB2	*Tto1* and *PAL*	Sugimoto et al., 2000
DkMyb2	*DkANR* and *DkLAR*	Akagi et al., 2010
CmMYB1	*CmMYB1, CmNRT, CmNIR* and *CmGS*	Imamura et al., 2009

mechanism remains elusive. Very recently, it has been uncovered that the members of the MYB family involved in the responses to abiotic stresses are usually the targets of small RNAs. MicroRNA828 directly targets *AtMYB113* and *lbMYB*, which are involved in anthocyanin synthesis and wounding responses (Rajagopalan et al., 2006; Lin et al., 2012). Furthermore, microRNA828 triggers the production of *TAS4-siRNA81*(−) that targets *PAP1, PAP2* and *MYB113* in *Arabidopsis*, and forms an autoregulatory feedback with *PAP1* in sugar stress signaling pathway (Luo et al., 2012). sRNA8105 represses *lbMYB1* expression by targeting the first intron and mediating methylation of the *lbMYB1* gene in wounding (Lin et al., 2013b). Additionally, sequencing analysis suggested that the mRNAs encoded by many *MYB* genes are the miRNAs targets under aluminum stress in wild soybean (Zeng et al., 2012).

The regulation of MYB proteins at the protein level including ubiquitination, sumoylation and phosphorylation, is essential for their functions. PAP1 and PAP2, two R2R3-type MYB proteins involved in anthocyanin synthesis and stress defenses, are both transcriptionally and post-translationally regulated by the COP1/SPA1 complex (Maier et al., 2013). AtPHR1 is sumoylated by AtSIZ1 in the regulation of Pi starvation responses (Miura et al., 2005). *AtCCA1*, an ortholog of *ZmCCA1* induced under Pi deficiency, is phosphorylated by Casein kinase2 (CK2), which is important for the DNA-binding activity of AtCCA1 (Daniel et al., 2004; Lin et al., 2013a).

A reducing environment is required for the DNA-binding activity of most R2R3-MYB and 3R-MYB proteins because of the presence of conserved Cys residues. Conversely, oxidation suppresses the function of MYB proteins (Myrset et al., 1993). Two Cys residues in the R2 motif of the maize P1 form intramolecular disulfide bonds in oxidizing conditions, which interferes with the DNA-binding activity of P1 (Heine et al., 2004). Nitric oxide induces S-nitrosylation of Cys53of AtMYB2 and inhibits binding of AtMYB2 to the target genes (Serpa et al., 2007).

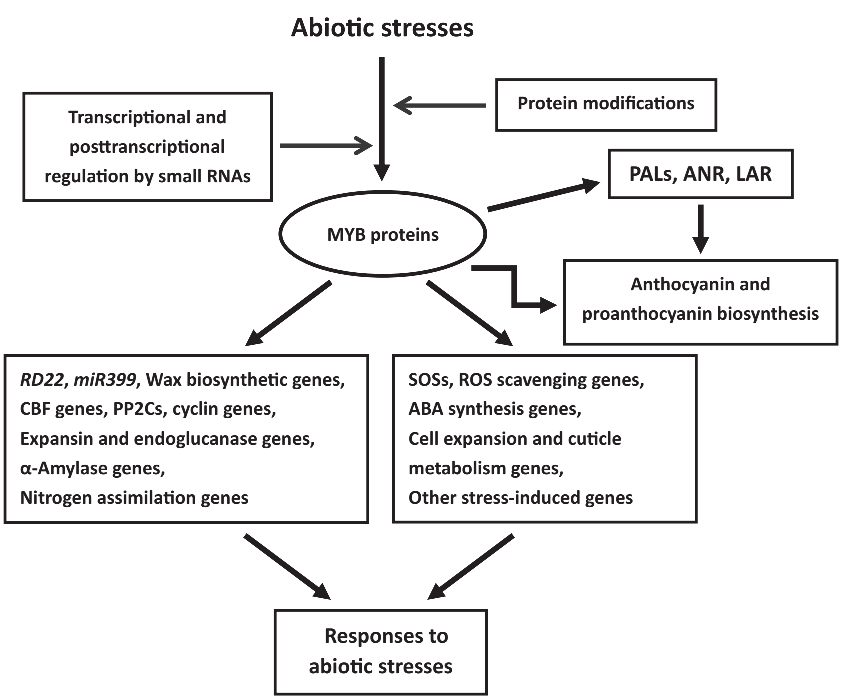

Fig. 2. MYB regulatory network in response to abiotic stress.

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The interaction of proteins is indispensable for the regulatory activity of some MYB proteins. OsMYB1 may regulate sugar signaling by interacting with itself to form a homodimer (Lu et al., 2002). The best-studied example of interaction is the MBW (MYB-bHLH-WDR) or MB (MYB-bHLH) complex (Feller et al., 2011). A R2R3-MYB protein AtMYB15 combines with a bHLH protein AtICE1, and they together bind to the *AtCBF3* promoter to regulate cold stress responses (Agarwal et al., 2006a). Flavonoid synthesis, essential for abiotic stress tolerance, is shown to involve several MBW complexes in different plant species, such as maize, rice, apple, cotton and *Arabidopsis* (Feller et al., 2011). For example, ZmC1 and ZmR are transcriptional coregulators of anthocyanin synthesis, and a few amino acids in the R3 repeat of ZmC1 determine the specificity of their interaction (Grotewold et al., 2000; Zimmermann et al., 2004). PAP1/PAP2 interacts with TTG1 and TT8/GL3/EGL3 to form a MBW to regulate anthocyanin synthesis, and AtMBL2 is a negative regulator competing with PAP1/PAP2 (Baudry et al., 2004; Dubos et al., 2008).

6. Conclusion and perspectives

Phylogenetic, structural and functional analyses revealed that there are many homologues of MYB proteins with conserved domains, which have similar functions and activities in divergent plant species (Table 1). A large number of MYB protein genes are induced or repressed in response to diverse abiotic stresses (Table 2). The members of the MYB family involved in the response to abiotic stresses are usually the targets of small RNAs. The regulation of MYB proteins at the protein level, including ubiquitination, sumoylation, phosphorylation and oxidation/reduction state, is essential for their functions. The interaction of proteins is indispensable for the regulatory activity of some MYB proteins (Fig. 2).

MYB proteins are shown to be involved in the regulation of numerous stress-related genes directly or indirectly in response to abiotic stresses, some of which are direct targets of MYB proteins (Table 2). The best-documented case for the roles of MYB proteins in the regulation of abiotic stressesis anthocyanin synthesis, where the upstream, downstream and coregulators of MYB proteins have been identified. Diverse abiotic stresses cross-talk with one another in the regulation of anthocyanin biosynthesis, in which MYB proteins play essential roles by regulating the expression of a large number of anthocyanin biosynthetic genes. In addition to anthocyanin biosynthetic genes, many stress related genes were also shown to be targets of MYB proteins in response to abiotic stresses (Fig. 2).

Although abundant information has been accumulated on the mechanisms underlying functioning of MYB proteins in abiotic stress responses, deciphering the upstream and downstream events and drawing a complete picture of MYB proteins in abiotic stress responses remains a huge task.

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